Forest Ecology and Management 603 (2026) 123469

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Severe fire has impacted populations of the California spotted owl more than fuels management or drought-related tree mortality

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ARTICLE INFO

Keywords:
Occupancy modeling
Bioacoustics
Fuels management
Spotted owls
Wildfire
Drought

ABSTRACT

Reducing fuel densities is the primary tool available to improve forest resilience to intensifying disturbance, but implementation is constrained by concern of effects to mature-forest associated species, such as spotted owls (*Strix occidentalis*). While the negative effects of severe fire on spotted owls are well studied, the influence of drought and fuels management on populations is uncertain, impeding fuels management. We integrated a novel dataset of California disturbance history with passive acoustic monitoring to compare the effects of severe fire, drought, and fuels management over 13 years on spotted owl occupancy across the Sierra Nevada, California, USA. Spotted owls were less likely to occupy 4 km^2 survey sites with a greater proportion of forest that burned at high severity and sites with a greater proportion of "heavier" fuels management (>25 % canopy reduction) but were insensitive to the proportion of "lighter" fuels management (<25 % canopy reduction) at sites. Across 7161 sites in the Sierra Nevada, severe fire resulted in an estimated loss of 482 occupied sites compared to only 65 lost from heavier treatments, owing to the limited implementation of fuels management in the region. Conversely, spotted owls were more likely to occur at sites containing a greater proportion of drought or other canopy reducing disturbance, presumably because of foraging opportunities facilitated by heterogenous forest conditions. Thus, recent severe fire has had a greater negative effect on spotted owls than fuels management, underscoring the potential benefits of increasing the pace and scale of fuels management for promoting both forest resilience and conserving mature-forest species.

1. Introduction

Around the globe, forests are rapidly changing due to resource extraction and climate-induced shifts in disturbance regimes (Hansen et al., 2013; Hughes, 2003; Seidl et al., 2017). In turn, changes in forest structure and composition are having profound effects on mature-forest-associated species (Bonnot et al., 2018; Wich et al., 2003; Williams et al., 2003). Species reliant on mature forests are among the most affected by compositional and structural forest changes given their dependence on elements of forest structure that can take decades to centuries to regenerate, such as large trees (Lindenmayer et al., 2012; Lindenmayer and Laurance, 2017). In addition, as mature-forest species are often restricted to relatively narrow habitat conditions, yet may be locally abundant within those conditions, effects of change in their habitat can be difficult to attribute over broad spatial scales. Given clustered abundance of mature forest specialists in suitable habitat, localized surveys may not capture small, but meaningful, changes in the broader population. Therefore, mitigating the effects of shifting disturbance regimes and land use on mature-forest species at broad scales can be challenged by uncertainties in which changing environmental factors are impacting populations, and how.

The spotted owl (*Strix occidentalis*), which uses mature forests for nesting, roosting, and often foraging (Jones et al., 2018; Ward and Noon, 1998; Zulla et al., 2022) is among the most well-studied wildlife species globally (Lõhmus, 2004; Gutiérrez, 2008). As such, the spotted owl resides at the center of many forest planning efforts across western North

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https://doi.org/10.1016/j.foreco.2025.123469
Received 30 June 2025; Received in revised form 17 December 2025; Accepted 19 December 2025
Available online 30 December 2025

America. Within seasonally dry forests, such as those in the Sierra Nevada, California, California spotted owl (*Strix occidentalis occidentalis*) habitat has experienced substantial change over the past century due to shifting disturbance regimes and land use changes. Post-colonial exclusion of Indigenous fire and suppression of natural ignitions, coupled with the selective harvesting of large trees, has resulted in forest densification and homogeneity biased toward smaller, shade-tolerant and fire-intolerant trees (Collins et al., 2017; Taylor et al., 2016). This densification, combined with climate warming, has increased the intensity, frequency, and magnitude of fire and drought (Crockett and Westerling, 2018; Stephens et al., 2018; Westerling et al., 2006). Large, severe fires now define forest structure across the Sierra Nevada (Cova et al., 2023) killing a high proportion of mature trees and converting forest to shrubland over increasingly large areas (Steel et al., 2022). Indeed, several recent studies have demonstrated that large patches of severe fire have persistent negative impacts on spotted owl habitat and populations (Jones et al., 2016, 2021b; Kramer et al., 2021; McGinn et al., 2025).

While the effect of severe fire on spotted owls is well documented, the impacts of drought-related tree mortality on spotted owls have not been assessed. Increased severity and frequency of drought conditions combined with intensified tree competition for water due to forest densification has induced landscape scale water stress over the last two decades, particularly in the southern Sierra Nevada (Stephens et al., 2018). Prolonged drought can exacerbate bark beetle outbreaks and associated tree mortality (Kolb et al., 2016) and promote fire due to resulting dry fuel (Steel et al., 2022; van Mantgem et al., 2009). While bark-beetle induced tree mortality is a natural disturbance agent in the Sierra Nevada and can create mosaics of age-classes in mature-forests, drought-driven outbreaks can result in mass tree mortality, often affecting large-diameter trees most acutely due to their greater water needs (Steel et al., 2022; Stephenson et al., 2019). Indeed, bark beetle outbreaks have caused more tree mortality than fires in the Southern Sierra Nevada in recent decades (Hicke et al., 2016), highlighting the need for research on the effects of drought-related tree mortality on mature forest species. Further, extensive tree mortality also increases the risk of fire in the Sierra Nevada by increasing fuel loads and fuel continuity, inextricably linking the direct effects of drought to its indirect effects via high severity fire (Cansler et al., 2024; Crockett and Westerling, 2018; Keen, 1929; Stephens et al., 2022).

In response to the rise in disturbance severity, land managers are striving to increase implementation of management to reduce fuels (dead/down debris, shrubs, and small/medium diameter trees) across the Sierra Nevada to promote resilience to severe fire, reduce drought-related tree mortality, and reduce tree densities (North et al., 2022; Stephens et al., 2020). Within dry, frequent-fire forests, such as those in the Sierra Nevada, many studies have shown that reducing surface fuels via mechanical or hand thinning can reduce post-fire tree mortality, lower landscape-scale fire severity, increase post fire seedling regeneration, and increase post-fire heterogeneity (Cansler et al., 2022; Liang et al., 2018; Stephens et al., 2009, 2020; Tempel et al., 2015; Tubbesing et al., 2019). Given spotted owls prefer to forage in areas with denser understory, where larger-bodied prey are abundant (Hobart et al., 2019; Tempel et al., 2015; Ward and Noon, 1998), thinning has the potential to negatively impact spotted owl habitat in the short-term by removing ladder fuels and surface vegetation. Some studies have detected negative effects of fuels management on spotted owl occupancy and nocturnal habitat use, but these were limited in temporal scales, spatial scales, and sample size, and were unable to distinguish among different types of management (Gallagher et al., 2019; Stephens et al., 2014; Tempel et al., 2015). In contrast, some studies have found slight positive or neutral effects of fuels management on spotted owls, though these studies were also limited in sample size (Irwin et al., 2015, 2013; Lee and Irwin, 2005). Along with financial and access-based constraints, concern over the effects of fuels management on spotted owls is restricting the pace and scale at which these practices are implemented (Collins et al., 2010; Kramer et al., 2021). As such, fuels management implementation in California is insufficient to meet California's restoration goals (Knight et al., 2022). Despite several decades of research, the relative effects of intensifying disturbance and the management necessary to reduce severe disturbance in spotted owl habitat remains uncertain – embodying the dilemma confronting the conservation of mature-forest species in general.

Here, we leveraged a Sierra Nevada-wide passive acoustic monitoring program and a novel dataset of disturbance history within the Sierra Nevada to compare effects of three disturbance types on spotted owls: severe fire, drought-related tree mortality, and fuels management. Because spotted owls use complex mature forest for roosting, nesting, and foraging, we hypothesized that the disturbance type exerting the most substantial influence on prevalence of large-diameter trees, canopy complexity, and understory density will have the greatest effect on spotted owl site occupancy. Thus, we predicted that the proportion of a site that has burned at high severity will have a greater negative impact on occupancy than the proportion of a site that experienced drought-related tree mortality or fuels management, given severe fire's impacts on all three metrics of forest structure. We also predicted that drought-related tree mortality will have a greater negative impact on site occupancy than fuels management as drought-related tree mortality most significantly affects large trees whereas fuels management typically retains large trees. Further, we predicted that more intense management with a greater reduction in canopy cover would have a greater negative impact on site occupancy than less intense management with a lesser reduction in canopy cover. At the population level, given the limited extent of fuels management in the Sierra Nevada, we predicted that severe fire and drought-related tree mortality have negatively impacted the number of occupied sites to a greater extent than fuels management. Finally, we compared the extent of severe fire and drought-related tree mortality and determined their relative effects on the estimated number of occupied sites across the study area. This study is the first to effectively compare the relative effects of the primary agents of forest change in the Sierra Nevada.

2. Methods

2.1. Study area

We conducted ecosystem-scale passive acoustic monitoring across the western slope of the Sierra Nevada, California in 2021 and 2022. The western slope is comprised of woodland and chapparal at low elevations dominated by *Quercus* species, that transitions to mixed-conifer forest at mid elevations, dominated by *Pinus* species, and *Abies* dominated subalpine forest at high elevations (Steel et al., 2015). Following over a century of fire suppression, forests of the Sierra Nevada currently have higher stem densities per hectare, higher densities of smaller-sized trees, and a greater proportion of shade-tolerant tree species (Knapp et al., 2013). The Sierra Nevada climate is characterized as Mediterranean, with warm, dry summers and cool, wet winters. Acoustic surveys spanned almost all suitable spotted owl habitat, entailing 28,644 km^2 across seven national forests (80.5 %), private land (18.1 %), and land owned by other entities (1.4 %; Kelly et al., 2023), with elevation ranging in the study areas from 226 to 3985 m. This area was overlayed with a grid of 4 km^2 hexagonal sites, the approximate size of spotted owl territories (Fig. 1; Wood et al., 2019). The total sampling grid includes 7161 sites, and we sampled a total of 758 sites and 776 in 2021 and 2022 respectively, with 705 sites sampled in both years.

2.2. Acoustic sampling

We deployed autonomous recording units (ARU; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) in non-contiguous sites to reduce the chance of detecting individual spotted owls in adjacent sites (i.e., reduce "ecological" false detections; Berigan and Jones

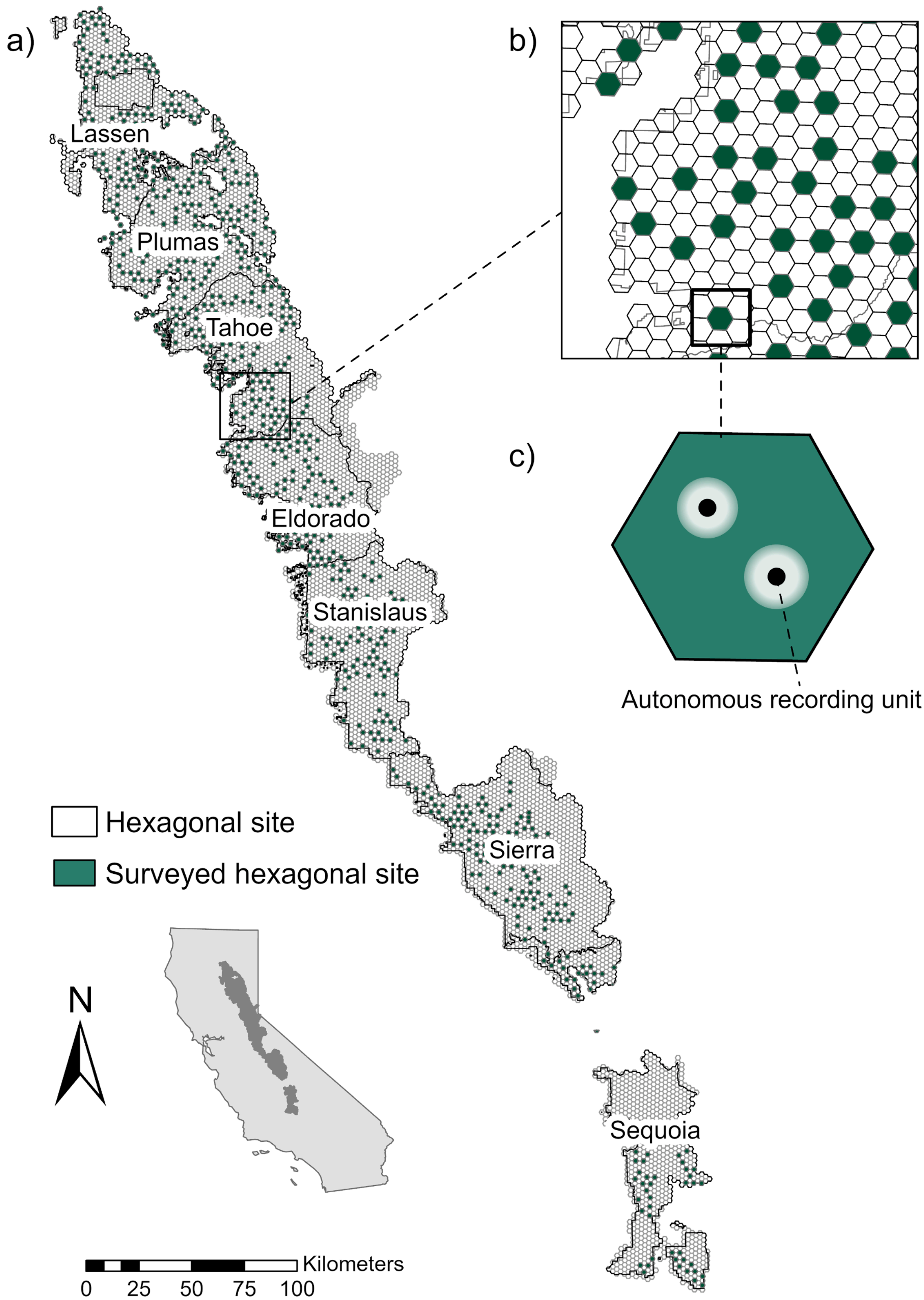

Fig. 1. Location of the a) bioacoustic monitoring study area overlayed with the hexagonal survey grid, b) surveyed sites in green, and c) autonomous recording units across seven national forests in the Sierra Nevada, California.

et al., 2019). Depending on road and trail access, one to four, but generally two ARUs were placed in a site, at least 500 m from each other and 250 m from the hexagonal site border. We attached ARU's to trees around chest height in acoustically advantageous locations within hexagonal sites (e.g. along ridgetops) and programmed the units to record overnight from 18:00–09:00 PDT. We deployed ARUs between early April and mid-July and recorded for five weeks continuously, with the entire deployment period spanning from May 03 – July 19 for 2021 and April 07 – August 08 for 2022. ARUs had a single omni-directional microphone and were programmed to record at a sample rate of 32 kHz with + 33 dB gain and 16-bit resolution.

To identify spotted owl vocalizations, we used audio data from 20:00–6:00 PDT, totaling 10 h per night. Surveyed hexagonal sites were treated as the sampling unit such that detections were pooled across ARUs within sites. We analyzed all audio using BirdNET, a deep convolutional neural network that provides a unitless prediction score for each 3 s interval of audio data that ranges from 0 to 1 representing the algorithm's confidence that a species' vocalization was recorded. We used a customized version of BirdNET which was overfit to the vocalizations of Sierra Nevada species, as well as the recording hardware and settings used in this project (Kahl et al., 2021). Following Kelly et al. (2023), all predictions with a score > 0.989 were verified by manually review in Raven 2.0 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2023). False-positives and audio determined to contain imitated spotted owl vocalizations (as part of playback surveys conducted by other groups) were removed (Berigan et al., 2019; Reid et al., 2021). Thus, we only worked with confirmed true-positive spotted owl detections.

2.3. Disturbance data

We developed a spatially- and temporally-explicit disturbance dataset that differentiates between wildfire, fuels management, and drought/other at 30 m resolution, detailed in Kramer et al. (2025). Briefly, we describe the methods used to develop each disturbance component relevant to this analysis.

We calculated fire severity at a 30-meter resolution following Cova et al. (2023) and Parks et al. (2019), and obtained fire perimeters from the California Department of Forestry and Fire Protection Fire and Resource Assessment Program (CALFIRE FRAP). These fires include wildfire from both non-prescribed human and natural ignitions, but prescribed fire was included in the forest management dataset (see below). We classified a given pixel as high severity when the composite burn index (CBI) was ≥ 2.25, consistent with severity classification described by Miller et al. (2009) and Miller and Thode (2007).

To characterize patterns in drought or other canopy reducing disturbance and intensity of fuels management, we used the Ecosystem Disturbance and Recovery Tracker (eDaRT) Mortality Magnitude Index (MMI; (Koltunov et al., 2020; Slaton et al., 2024). The eDaRT algorithm uses Landsat imagery to estimate the probability that canopy cover changed at 8- or 16-day intervals at 30 m resolution. The MMI product uses eDaRT to estimate the magnitude of these disturbances on an annual time scale, with any given pixel ranging from 0 to 100 representing an estimated 0–100 % loss of canopy cover.

We mapped fuels management activities using a modified version of the USFS Activity Tracking System (FACTS), which contains spatial records of all USFS activities (USDA) and classified intensity using eDaRT MMI. First, from FACTS we filtered for entries with fuels management codes to test our predictions that fuels management impacted spotted owls, accounted for activities lacking completion data, and applied temporal buffers that capture 91 % of change on the landscape due to fuels management activities (Kramer et al., 2025). Importantly, because FACTS data only describe management activities on land managed by the USFS, we were only able to account for management on USFS-managed land. As such, we used a land ownership layer that classed USFS-managed and non-USFS-managed land and included the proportion of USFS-managed land as an occupancy covariate to account for forest management on non-USFS-managed land, primarily even aged commercial timber harvesting, (see *Occupancy modeling* section). We characterized fuels management pixel intensity as "lighter" (lesser canopy cover reduction) versus "heavier" (greater canopy cover reduction) using pixel-scale eDaRT MMI values. For instance, an MMI score of 25 corresponds to 25 % canopy loss within a pixel, calculated on an annual basis, and summed across the 13-year span for a survey site. We considered several potential MMI thresholds through visual inspections of NAIP imagery and we ultimately selected a threshold of 25 MMI (25 % canopy cover reduction) as it yielded (1) a visible distinction between more and less intensive forest management activities (Figs. 2) and (2) a reasonable number of non-zero values for both lighter and heavier intensity management at the scale of the 4 km^2 hexagonal survey sites.

We used MMI data to delineate areas of drought or other canopy reducing disturbance when a pixel was not within a fire perimeter or a fuels management area. We visually assessed several MMI thresholds using the National Agriculture Imagery Program (NAIP), beginning with a minimum threshold of 10 (Slaton et al., 2024) and ending at a threshold of 20, where MMI thresholds stricter than 20 did not provide a reasonable sample size of non-zero values. We ultimately used a minimum MMI threshold of 12, equivalent to a 12 % canopy reduction within a pixel, as it visually matched a known gradient in drought (Fettig et al., 2019) and provided a large enough sample size of sites with non-zero values. We refer to these pixels as "drought/other" as they represent areas with high levels of canopy cover loss which could be due to drought or other canopy reducing disturbance types (e.g. insect or disease damage unrelated to drought, blowdown, or landslides). Through visual inspections of areas mapped as drought/other against aerial imagery and knowledge of the disturbance history of the area (Asner et al., 2016; Fettig et al., 2019), we were confident that the majority of this mortality was due to drought associated agents. Although the MMI data covered all land ownerships, we could not differentiate between drought or other and forest management on non-USFS managed land (see below), so as with fuels management, we were only able to estimate drought/other on USFS managed land.

Finally, we compiled annual rasters for each disturbance component across a 13-year span (2008–2020 and 2009–2021). Although a pixel could only be assigned a single disturbance type for any given year, pixels in the 13-year composite could have experienced multiple disturbances. For each sampled 4 km^2 site, we calculated the proportional area affected by each disturbance type for each 13-year span, with all disturbance types individually ranging from 0 to 1 corresponding to 0–100 % of the site disturbed (Fig. 2).

2.4. Occupancy modeling

We tested whether site-level, survey-level, and annual covariates influenced detection and occupancy probabilities (Mackenzie et al., 2002). To do so, we fit a single model using the package "unmarked" (Fiske, 2011) in Program R (R. Core Team, 2025). We used a single-season stacked occupancy modeling framework and considered the effect of year on both detection and occupancy probabilities (Burnett and Roberts, 2015; Fogg et al., 2014; MacKenzie et al., 2002) given we were more interested in regional patterns in occupancy than extinction and colonization dynamics and our surveys were limited to two years. By "stacking" yearly detection histories we increased our effective sample size, with each site and year combination functioning as an independent site and thus supporting the estimation of a greater number of predictor variables. This method has the potential to underestimate error by pseudo-replicating sites; however, we felt this method was preferrable to a multi-season model as we were focused on identifying clear disturbance associations and we included year as a fixed effect on occupancy and detection to account for variation between years.

We divided the continuous summer season of sampling into eighteen

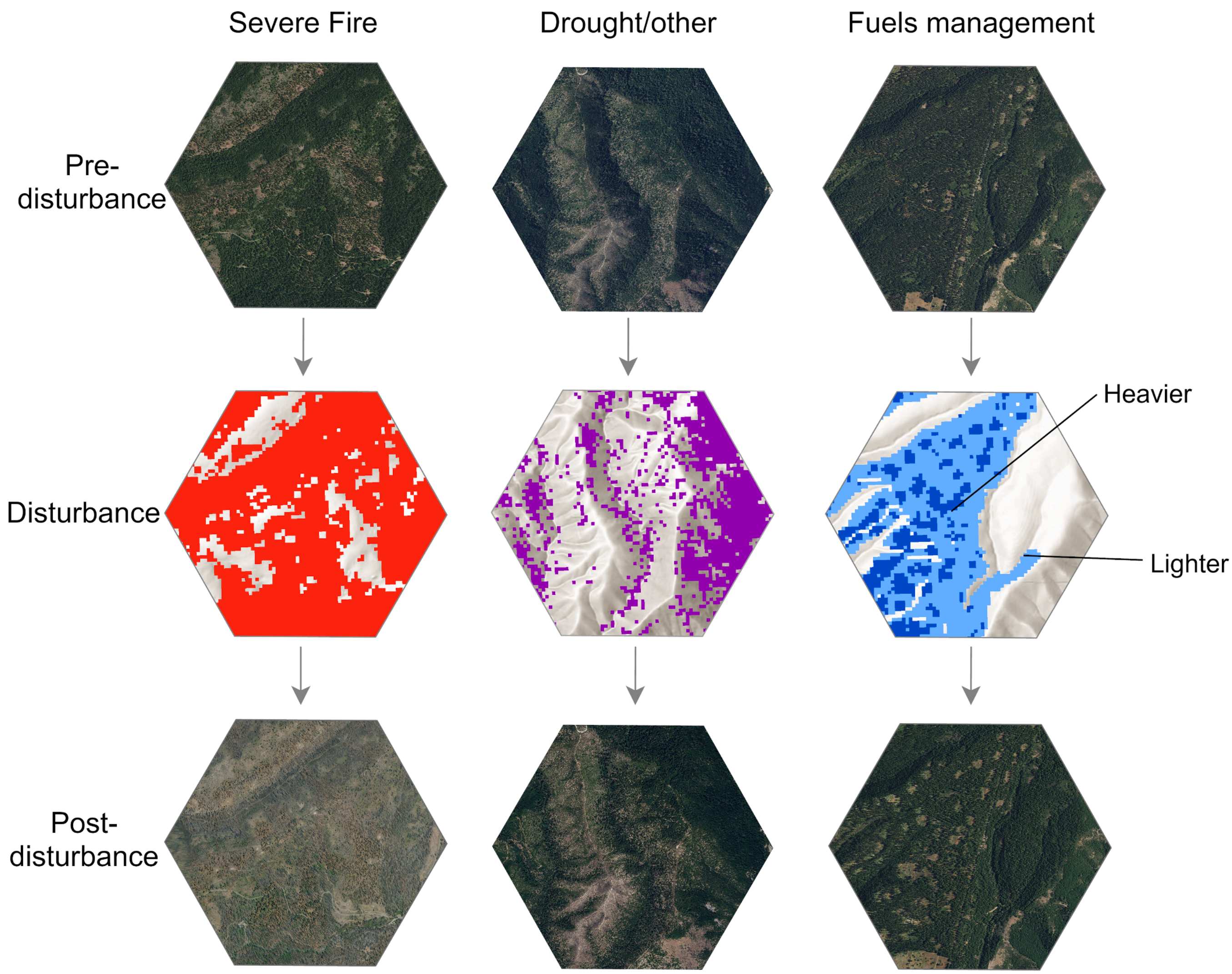

Fig. 2. NAIP imagery of survey sites before and after each disturbance type. Canopy loss attributed to drought/other is difficult to see with the naked eye, highlighting the need for eDaRT and MMI. Highlighted areas indicate the disturbance footprint identified from the Kramer et al. (2025) dataset. Imagery brightness was increased by 10 % to highlight disturbed areas.

week-long secondary sampling periods (*j*), or visits. Survey effort per visit (up to 80 h of audio per unit) was included as a detection covariate; a visit was considered null if no audio was recorded. For each site, we used a two-night detection criteria where a site (*i*) was assigned a 1 if there was a confirmed vocalization within that visit, as well as on at least one other different night within a season (Kelly et al., 2023), or assigned a 0 if these criteria were not met. This method reduced the likelihood of an ecological false-positive and increased the likelihood that the vocalization was from resident owl (Berigan et al., 2019). Following previous analyses of this acoustic dataset, we used an established global detection model that included survey effort (hours surveyed per visit within a site), secondary sampling period date (mean sampling date of each visit), and categorical year as effects on detection (*p*) probability (Winiarski et al., 2024; Winiarski et al., in press). We modeled the probability of site occupancy using the following topographic and landownership variables: the proportion of USFS land, elevation, and latitude (in California Albers projection). Within the Sierra Nevada, bird species distributions vary by latitude and elevation (Saracco et al., 2011; Siegel et al., 2011; Winiarski et al., 2025). Therefore, to control for the effect of latitude on elevation, we modeled a linear relationship (elevation ∼ latitude) and used the residuals to estimate "latitude-corrected elevation". In addition, we included a quadratic term for secondary sampling period date, to account for potential peaks in calling activity during the breeding season, and for latitude-corrected elevation to account for peaks in occupancy along elevation gradients. To avoid confounding our disturbance covariates, we did not use any metrics of forest-structure in our model as our disturbance data was more recent than the available forest-structure dataset. We Z standardized all continuous covariates. We modeled the probability of site occupancy using the proportion of a site that experienced severe fire, drought/other, heavier management, and lighter management over the prior 13-years. We drew inferences from a global site occupancy model that included all the aforementioned covariates representing factors potentially affecting detection and occupancy probabilities, assessing the statistical significance of each estimated parameter based on overlap of the 95 % confidence intervals with 0.

2.5. Estimating the number of occupied sites lost or gained to disturbance and management

Using our occupancy model, we estimated the total number of occupied sites lost or gained in association with each disturbance or management type across the entire 7161 site sampling grid for the 2009–2021 period. Our framework was analogous to the "scope for management" approach introduced by Norris and Mcculloch (2003) to assess the effects of environmentally-induced changes in survival and reproductive probabilities on population numbers. To do so, we first estimated predicted occupancy (Ψ) for each site i given the area that was disturbed (or managed for fuels) where D_i represented proportional disturbed area within a site:

$$logit(\Psi_{i.disturbed}) = \beta_0 + \beta_1 D_i$$

We then estimated predicted occupancy for each site assuming no disturbance had occurred (i.e., $D_i = 0$):

$$logit(\Psi_{i.undisturbed}) = \beta_0$$

Both predictions were made assuming observed values at site i for the topographic and landownership covariates included in the site level occupancy model. Then we estimated the difference in predicted occupancy for each site i between the disturbed and undisturbed scenarios ($\Delta\Psi_i$) as follows:

$$\Delta\Psi_i = \Psi_{i.undisturbed} - \Psi_{i.disturbed}$$

By summing the difference between predicted site occupancy of disturbed sites assuming disturbance did versus did not occur, we estimated the expected number of occupied sites lost or gained from each type of disturbance ($\Delta\ \Psi_{total}$) as:

$$\Delta\ \Psi_{total} = \sum_{1=1}^{n} \Delta\Psi_i$$

We also estimated the proportional change in occupancy, $\Delta\ \Psi_{proportional}$, caused by each disturbance across the 13-year period by dividing $\Delta\ \Psi_{total}$ by the sum of predicted occupancy assuming no disturbance had occurred:

$$\Delta\ \Psi_{proportional} = \frac{\Delta\ \Psi_{total}}{\sum_{1=1}^{n} \Psi_{i.undisturbed}}$$

3. Results

3.1. Passive acoustic surveys

In 2021, we deployed 1476 ARUs across 758 four-km^2-hexagonal survey sites and in 2022, we deployed 1616 ARUs across 778 hexagonal survey sites, with 705 sites sampled in both years out of the total 7161 hexagonal cells within the grid. In total, 490,823 and 515,692 h were recorded in 2021 and 2022 respectively. Based on the two detection night criteria, naïve occupancy (the proportion of sites with a spotted owl detection) was similar in 2021 (0.293) and 2022 (0.281). When corrected for detection, mean occupancy was estimated as 0.245 and 0.259 for 2021 and 2022 respectively.

3.2. Disturbance mapping

The proportion of area experiencing heavy and light fuels management within hexagonal cells ranged from 0 to 0.495 and 0–0.993, respectively, with means of 0.023 (standard deviation (SD): 0.05) and 0.115 (SD: 0.146), respectively. The proportion of area experiencing drought/other within hexagonal cells ranged from 0 to 0.934, with an average of 0.228 (SD: 0.164), and the proportion area experiencing severe fire within hexagonal cells ranged from 0 to 0.998, with a mean of 0.163 (SD: 0.276).

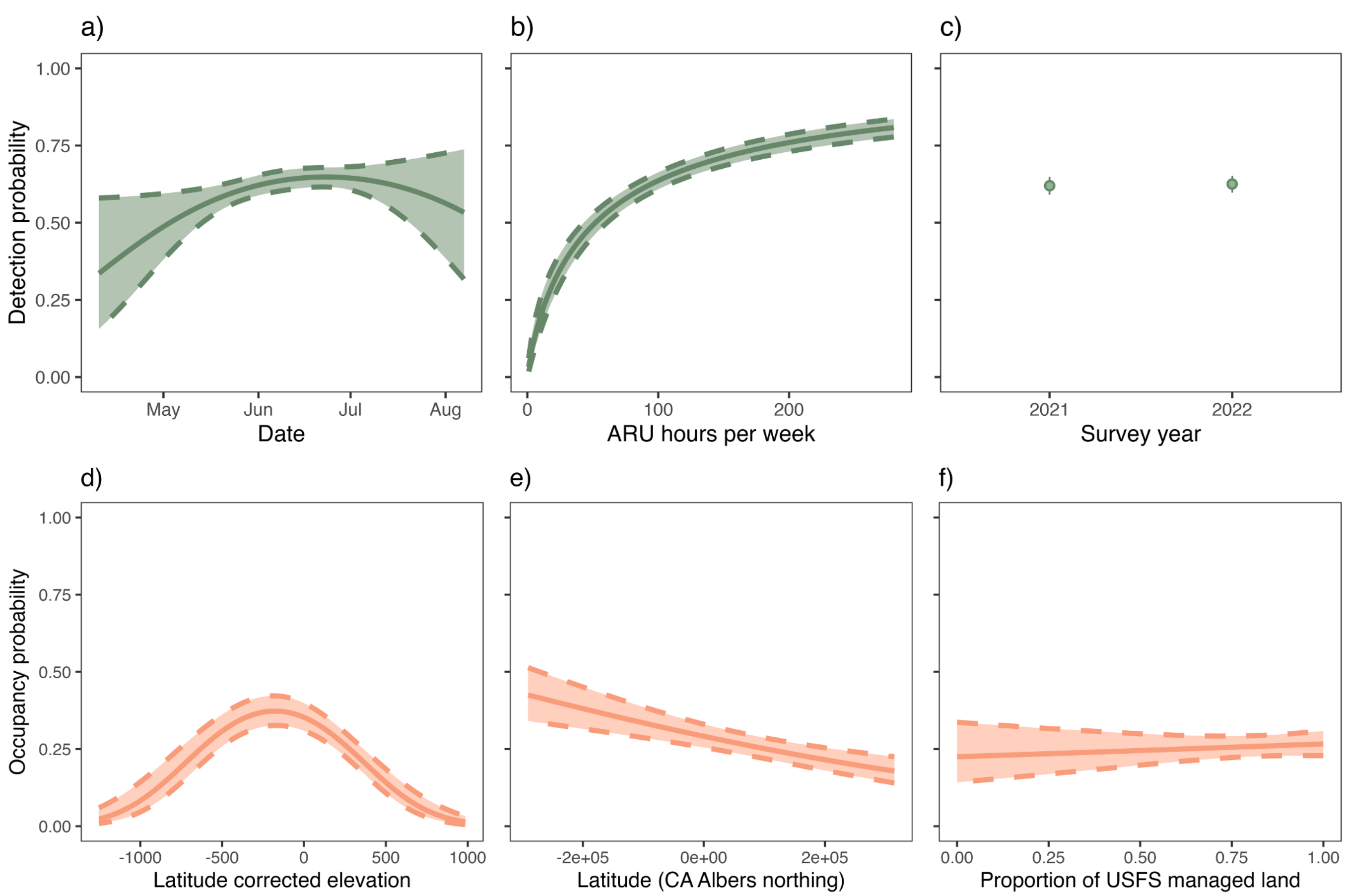

Fig. 3. Detection probabilities for a) mean survey date and b) survey hour per week and c) survey year and occupancy probabilities for d) latitude corrected elevation, e) latitude (CA Albers northing) and f) proportion of USFS land in a survey site where shaded bars represent predicted 95 % confidence intervals.

3.3. Site level occupancy analysis

3.3.1. Detection probability

Mean predicted detection probability across sites was 0.665 (95 % confidence interval (CI) [0.634 – 0.694]) and 0.670 (95 % CI [0.638 – 0.700]) in 2021 and 2022, respectively. The probability of detecting a spotted owls at a given site increased more survey effort (β: 0.571, 95 % CI [0.479 – 0.662]; Fig. 3b). Spotted owls were more likely to be detected in the middle portion of our seasonal survey period as indicated by a positive linear (β: 0.590, 95 % CI [0.014 – 1.166]) and negative quadratic (β: −0.491, 95 % CI [-1.060 – 0.079]) relationship with mean date of the visit, with detection peaking around mid-June (Fig. 3a). Predicted seasonal detection probability of detecting an owl present at a survey site over a typical 5-week sampling period was 0.996 for both 2021 and 2022 (Fig. 3c).

3.3.2. Effects of topography and landownership on occupancy

Spotted owl occupancy peaked at low-to-mid elevation sites, after controlling for latitude (linear β: −0.400, 95 % CI [-0.556 - −0.235], quadratic (β: −0.590, 95 % CI [-0.749 - −0.431]; Fig. 3d) and was highest in the southern Sierra Nevada (β: −0.307, 95 % CI [-0.443 - −0.171]; Fig. 3e). Occupancy did not vary based on the proportional area of USFS landownership (β: 0.052, 95 % CI [-0.096 – 0.201]; Fig. 3f).

3.3.3. Effects of disturbance and management on occupancy

Spotted owls were less likely to occur at sites with more severe fire (β: −0.689, 95 % CI [-0.852 – −0.526] Fig. 4a) and sites where heavier management was implemented (β: −0.203, 95 % CI [-0.355 – −0.052]; Fig. 4c). We did not find support for an effect of lighter management on site occupancy; while the relationship was positive (β: 0.077, 95 % CI [-0.054 – 0.208] Fig. 4d), confidence intervals overlapped 0. In contrast, spotted owls were more likely to occur at sites with more drought/other (β: 0.341, 95 % CI [0.197 – 0.485]; Fig. 4b).

The negative effect of severe fire on spotted owl site occupancy was three times greater than the negative effect of heavier management on site occupancy based on the magnitude of the coefficients. However, this difference was likely attributable to the standardization of covariates where, for example, a 1 standard deviation change resulted in much

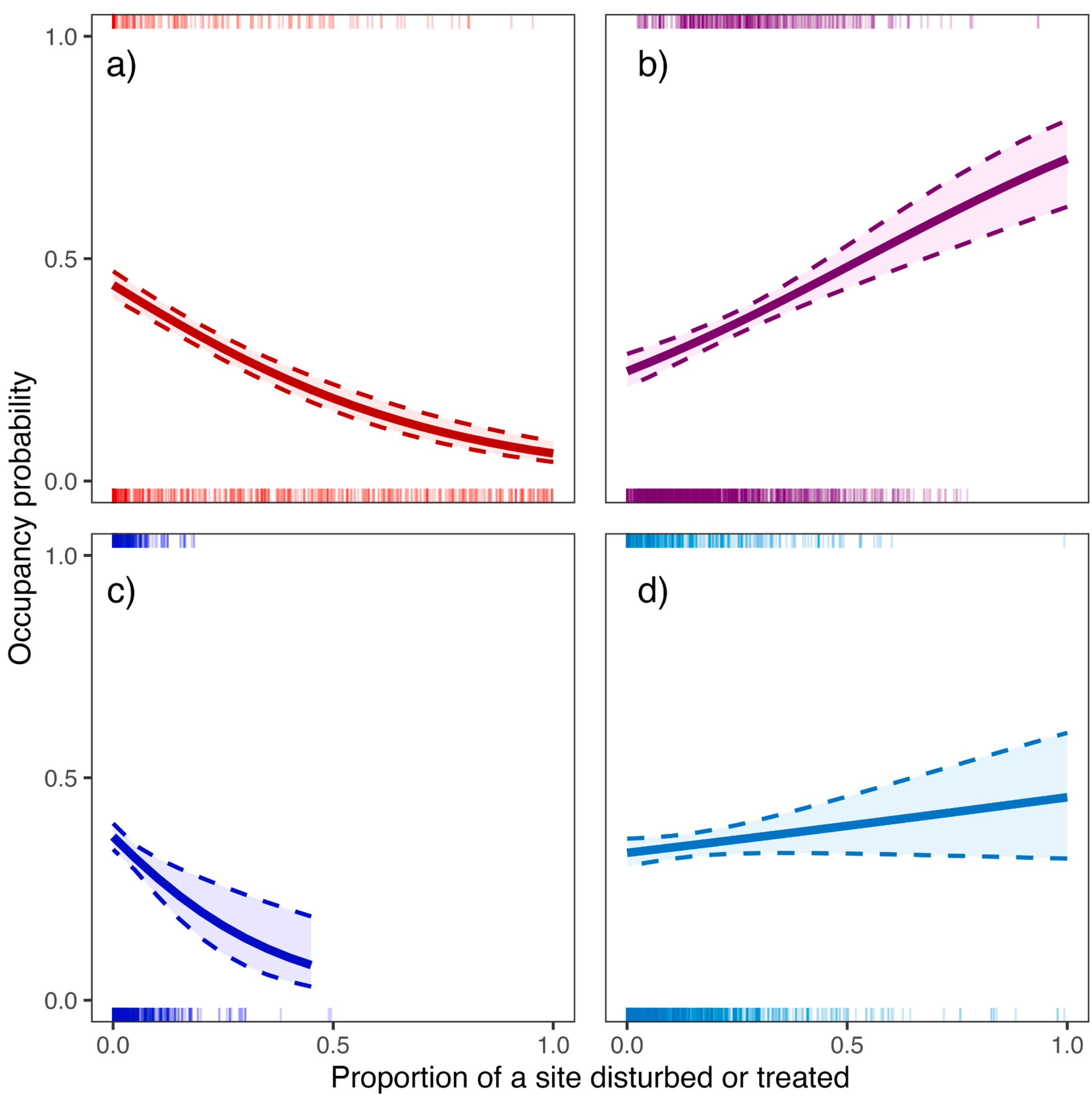

Fig. 4. Occupancy probability as a function of the proportion of a site that was a) severely burned, b) experienced drought/other, or c) heavier and d) lighter fuels management. Estimates end at sampled disturbance maximum. Shaded area indicates 95 % predicted confidence intervals. Rug ticks along the top indicate sites where spotted owls were detected, while ticks along the bottom indicate proportion of disturbance in sites where spotted owls were not detected.

smaller magnitude of change in the proportion of a site experiencing heavier treatment than it would in the magnitude of change in the proportion of a site experiencing severe fire. When all other variables were held constant at their mean values within the dataset, the maximum proportion of a site severely burned (0.998) led to a 0.379 decline in occupancy, from 0.441 to 0.063, while the maximum value of heavier management (0.495) led to a similar 0.302 decline in occupancy, from 0.368 to 0.066.

3.4. Total sites lost or gained to disturbance

When total gains/losses were averaged across all sites and then compared to estimated mean occupancy, severe fire led to a proportional decline($\Delta\,\boldsymbol{\Psi}_{proportional}$) in occupancy per site of 27.6 % (mean change ($\Delta\,\boldsymbol{\Psi}$) of −0.063 from 0.291 to 0.228 per site) while heavier management only led to a proportional decline in occupancy of 3.5 % (mean change of −0.008 from 0.236 to 0.228 per site). Drought/other led to a proportional increase in occupancy of 24.1 % (mean change of 0.055 from 0.173 to 0.228 per site) and lighter management led to a proportional increase in occupancy of 2.2 % (mean change of 0.005 from 0.233 to 0.228 per site).

Severe fire had the greatest influence on the estimated number of sites occupied by spotted owls ($\Delta\,\boldsymbol{\Psi}_{total}$), with an estimated loss of 482 occupied sites out of 7161 total sites (Table 1). By contrast, heavier management resulted in an estimated loss of only 65 occupied sites – more than 7 times fewer than the decline incurred by severe fire. This difference was in part attributable to the fact that heavier treatments were only implemented over only 2.3 % of the study area, whereas severe fire occurred over 16.3 % of the study area, over the past 13 years. Drought/other led to an estimated gain of 440 occupied sites and lighter management led to an estimated gain of 39 occupied sites (Table 1; Fig. 5). In Fig. 6, we provide map-based examples of lower occupancy in severely burned and heavy fuels management areas, and higher occupancy in areas with lighter fuels management and drought/other.

4. Discussion

4.1. Summary of results

Concern over the effects of fuels management on mature-forest associated species continues to impede efforts to promote forest resilience in the face of increasingly large and severe wildfires and drought-related tree mortality. Leveraging a large-scale passive acoustic monitoring program and a novel synthetic dataset mapping spatial and temporal patterns in forest disturbance and management, this study is the first to simultaneously assess the effects of implemented fuels management on a mature-forest associated species and compare these effects to the impact of severe fire and drought at a regional scale. Our results supported our hypothesis that recent high-severity wildfire has negatively impacted spotted owls more than fuels management. When summed across the study area, over the prior 13 years, severe fire led to a loss of 482 occupied sites, while heavier management led to loss of only 65 occupied sites and lighter management resulted in a gain of 39 occupied sites, out of the total 7161 sites. Further, despite suggestions of drought-related tree mortality as a threat to spotted owl conservation (Jones et al., 2021b), this study is the first to demonstrate that spotted owls are actually more likely to occur at sites with a greater proportion of drought/other, and adds to the growing body of literature on the effects of shifting disturbance regimes in western forests on old-forest associated species.

Table 1
Population-level results describing changes in occupancy from four different disturbance types. Mean change in occupancy probability caused by each disturbance or management type is equal to [average occupancy probability with disturbance] minus [average occupancy probability without disturbance]. Proportional change in occupancy is equal to the average change in occupancy caused by each disturbance divided by average occupancy. The total number of occupied sites lost or gained to each disturbance is the difference in occupancy between occupancy with and without each disturbance summed across all sites, rounded to the nearest whole number.

	Severe fire	Drought/ other	Heavier management	Lighter management
Average true occupancy – average predicted occupancy had each disturbance not occurred	0.228 – 0.291	0.228 – 0.173	0.228 – 0.236	0.228 – 0.223
Mean change in occupancy ($\Delta\,\boldsymbol{\Psi}$)	-0.063	0.055	-0.008	0.005
Proportional change in occupancy ($\Delta\,\boldsymbol{\Psi}_{proportional}$)	-0.276	0.241	-0.035	0.022
Number of occupied sites gained or lost ($\Delta\,\boldsymbol{\Psi}_{total}$)	-482	440	-65	39

4.2. Corroborating the negative effects of severe fire on spotted owls

As predicted, spotted owls were less likely to occur at sites with a greater proportion of forest that burned severely within the past 13 years - consistent with the large body of research on the relationship between spotted owls and fire. While spotted owls in the Sierra Nevada and other seasonally dry forests appear adapted to a frequent-fire regime consisting of mostly lower severity fire with relatively small patches of higher severity fire, many recent studies have demonstrated that spotted owls are ill adapted to increasingly severe, large, homogenous fire. For example, Jones et al. (2016) found a seven-fold increase in extinction probability at severely burned survey owl territories following the 2014 King Fire, with follow-up studies revealing persistent negative effects on nesting habitat and low territory recolonization up to two decades post severe fire (Jones et al., 2021b; McGinn et al., 2025). Moreover, large and homogenous severe wildfire eliminates spotted owl foraging habitat as foraging spotted owls typically avoid large patches of severely burned area and select for heterogenous areas burned at lower or mixed severity (Eyes et al., 2017; Jones et al., 2020; Kramer et al., 2021). Stable spotted owl populations in national parks characterized by partially restored fire regimes (Conner et al., 2013; Kramer et al., 2021) compared to declining populations in areas that have experienced large severe fires (Jones et al., 2021b; Winiarski et al., in press) indicate that territory-scale effects of wildfire dynamics have landscape and even regional scale population level effects; consistent with our finding that severe fire had the largest population level effect relative to fuels management and drought/other.

Thus, our study further dispels an incorrect narrative that spotted owls are insensitive to large severe fires. In the most comprehensive analysis at the time, Lee (2018) found that severe fire did not reduce spotted owl occupancy, vital rates, or nocturnal habitat selection – with potential analytical and methodology issues and inferences debated by Jones et al. (2020) and Lee (2020). However, all 9 studies published since Lee (2018), including this one, have documented significant adverse effects of severe fire on some measure of spotted owl population or foraging ecology (Brunk et al., 2025a; Jones et al., 2021b, 2020; Kramer et al., 2021; McGinn et al., 2025; McGinn et al., 2023; Schofield et al., 2020; Tempel et al., 2022; Winiarski et al., in press) including a recent large-scale meta-analysis involving 1514 northern and California spotted owl territories and 171 GPS tagged owls (McGinn et al. in review). By contrast no published papers have found large severe wildfire to be benign to spotted owls since the publication of Lee (2018). Some have suggested that declines in spotted owl populations can be attributed to post-fire salvage logging, but the amount of salvage logging is generally relatively small, particularly on public lands, with no or weaker effects than severe fire (Jones et al., 2021b, 2016; McGinn et al., 2025). Thus, the debate is settled – large severe fires pose a major threat

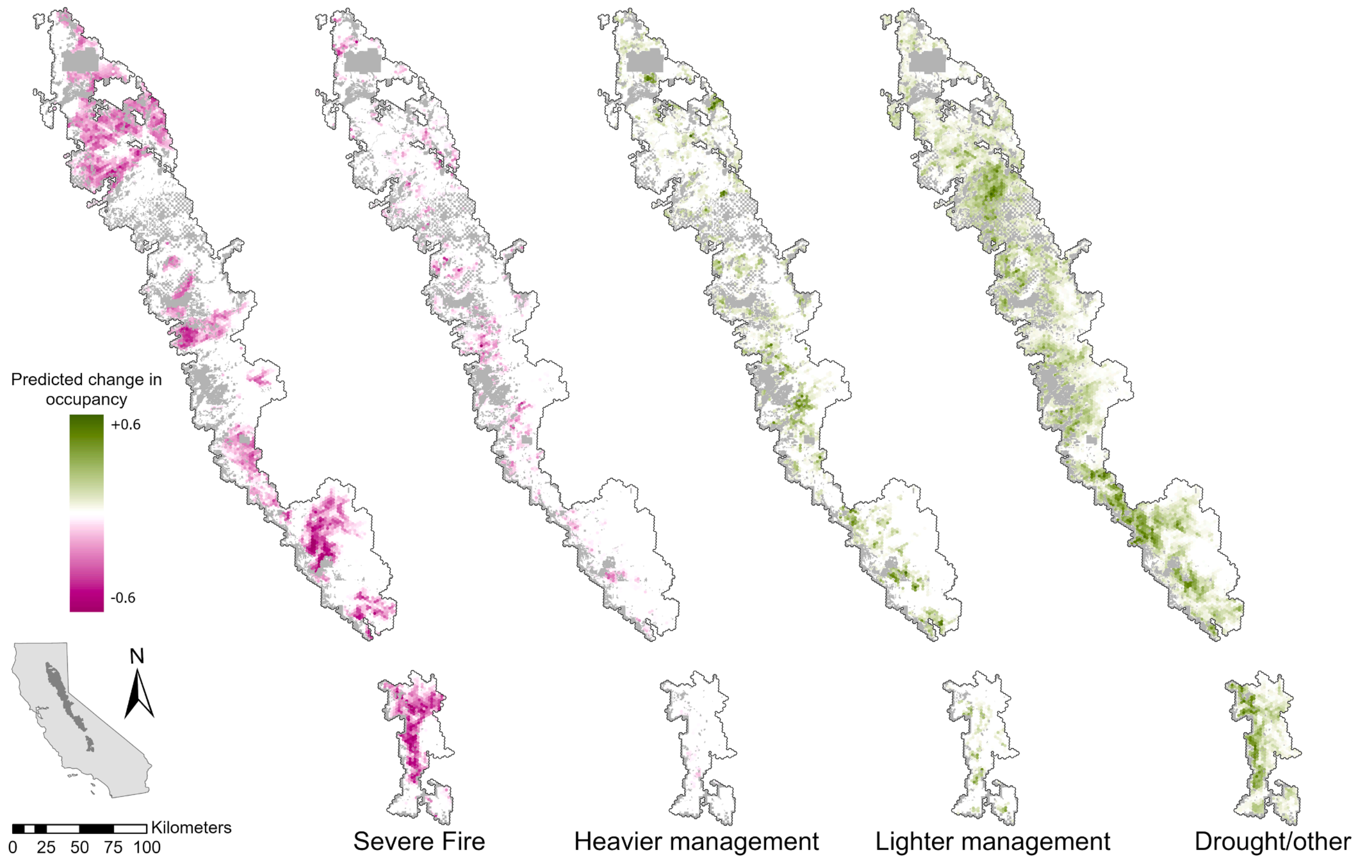

Fig. 5. Changes in occupancy caused by a) severe fire, b) heavier fuels management, c) lighter fuels management, and d) drought/other across the Sierra Nevada. Negative changes in occupancy are shown in pink, and positive changes are shown in green. Non-USFS land is shown in gray.

to spotted owls and forest restoration efforts may be needed to curb this threat (see also below).

4.3. Benefits of drought/other to spotted owls

While the adverse effects of severe fire on spotted owls are clear, the potential impacts of drought-related tree mortality on spotted owls have been uncertain. Drought and associated tree mortality are natural processes shaping seasonally dry forests, where under normal conditions, drought-related tree mortality can create a mosaic of seral stages and promote forest resiliency (Asner et al., 2016; Stephens et al., 2018). However intensifying drought events have led to mass tree mortality, leading to uncertainty in how mature-forest species will respond and how to manage drought-affected forests (Fettig et al., 2019). Contrary to our prediction, spotted owls were more likely to occur at survey sites with a greater proportion of drought/other. Given that our acoustically based detections were obtained from both crepuscular and nocturnal periods, when owls may be in roost or nest areas or quite far from them, we suspect that owls may be selecting for areas with greater proportions of drought/other as a result of improved foraging conditions. Specifically, following historical densification and homogenization of Sierra Nevada forests, drought-related tree mortality of some conifer trees may create more gaps and openings in the forest, and thus more fine-scale forest heterogeneity that may benefit larger-bodied prey such as dusky-footed woodrats (*Neotoma fuscipes*; Kuntze et al., 2023). Indeed, spotted owls have higher prey capture success, consume more woodrats, and deliver more prey biomass to nests in territories with more heterogenous forest conditions (Hobart et al., 2019; Wilkinson et al., 2023; Zulla et al., 2022). In contrast with high severity fire, drought-related tree mortality kills but does not eliminate trees, resulting in high remaining biomass. Dusky-footed woodrats are more likely to occur at sites with higher understory cover and dead and down debris (Kuntze et al., 2025), which may be enhanced by drought-related tree mortality. Moreover, hardwoods such as oaks (*Quercus* spp.), which provide masting food resources for prey, are more resilient to drought, but are also often overtopped by dense conifers. These species may increase in vigor as the canopy thins as a result of drought-related tree mortality, potentially also promoting foraging opportunities for owl prey species like the dusky-footed woodrat.

Despite the putative benefits of drought/other to nocturnally foraging spotted owls, drought could compromise other life-history activities and potentially lead to population declines over the long-term via compounded interactions with other disturbance effects. As a cold-adapted species, spotted owls typically spend warmer daytime hours roosting in mature forest stands characterized by cooler microclimates (Barrows, 1981). Drought-related tree mortality is typically biased towards larger trees in the Sierra Nevada (Steel et al., 2022; Stephenson et al., 2019), which reduces canopy cover and complexity, inevitably leading to warmer microclimates. McGinn et al. (2023) found that roosting spotted owls were regularly exposed to temperatures above their thermoneutral zone during heatwaves, with potentially adverse effects on populations. Thus, the potential immediate benefits of drought-related tree mortality to foraging success may be outweighed by long-term negative physiological effects, when considered in the currency of fitness. Drought-related tree mortality could also negatively impact spotted owls given dead woody biomass can amplify fire severity and post-fire tree mortality (Cansler et al., 2024; Crockett and Westerling, 2018; Stephens et al., 2022). As such, drought-affected forests may precipitate another trade-off where spotted owls benefit from increased foraging opportunities but experience greater loss of nesting and foraging habitat from drought-fueled severe fires. Clearly, more research is needed to understand the multi-faceted ways in which

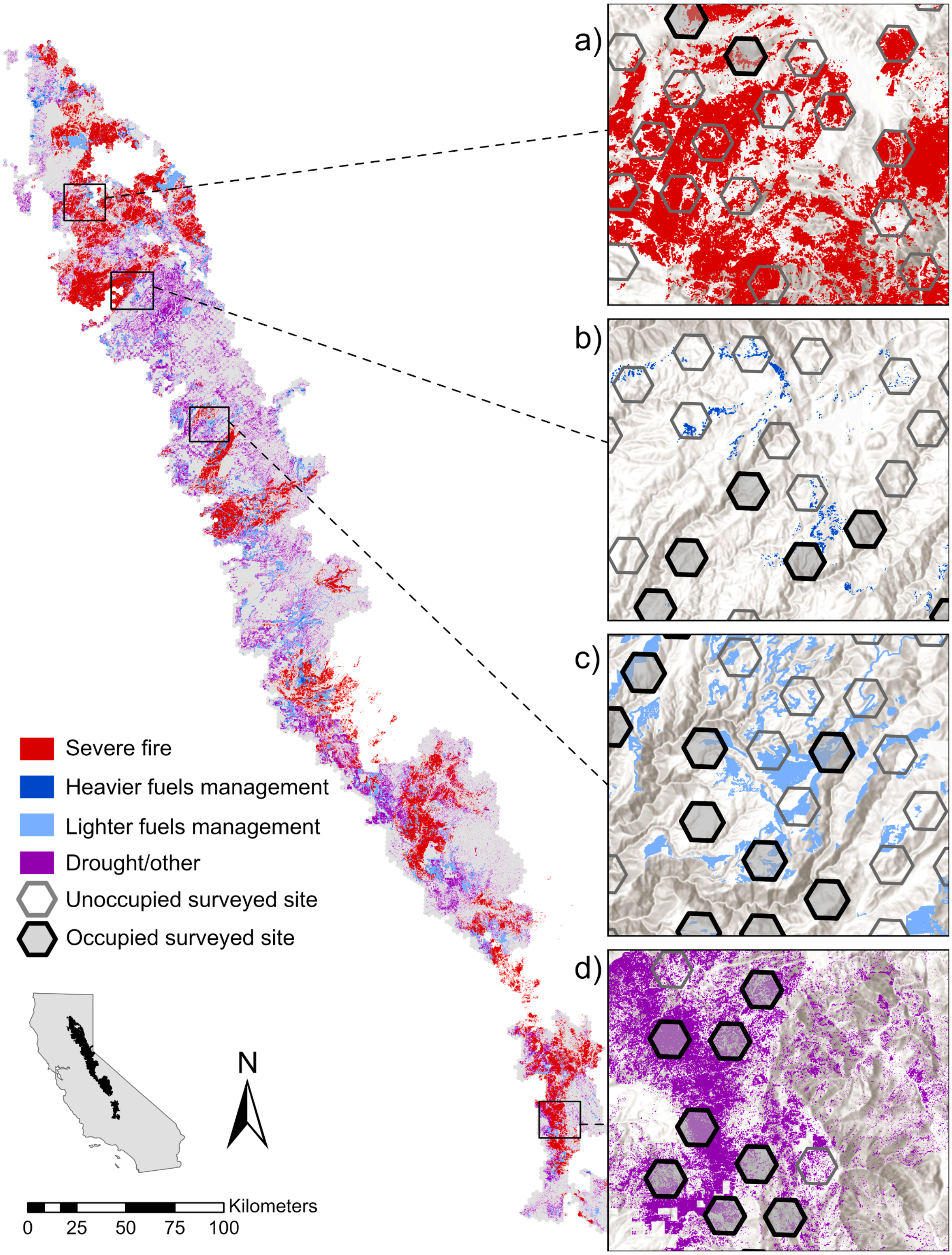

Fig. 6. a) High severity fire, b) heavier fuels management, c) lighter fuels management, and d) drought/other mapped across the monitoring grid with surveyed hexes in bold outline and color of hexes indicating occupancy status. Each zoomed in map contains only the relevant disturbance type.

drought affects spotted owls, biodiversity broadly, and, ultimately, drought-prone and drought-affected forests.

4.4. Fuels management effects depend on treatment intensity

Concern over the potential effects of fuels management on spotted owls has constrained efforts to promote resilient forests (Peery et al., 2017). Some previous studies have detected short-term negative effects of fuels management on spotted owl habitat (Tempel et al., 2015), nocturnal habitat use (Gallagher et al., 2019), occupancy (Seamans and Gutiérrez, 2007; Stephens et al., 2014; Tempel et al., 2022), and demographic rates (Tempel et al., 2014), while others found neutral or positive effects of fuels management on spotted owl space use (Irwin et al., 2015, 2013; Lee and Irwin, 2005). Yet inferences from these studies were limited by small sample sizes of territories with fuels management or ability to distinguish fuels management from other forest management activities or natural disturbances. Assessments of fuels management effects on spotted owls have also been challenged by limitations with the quality of available fuels management data, including inconsistences, errors, and missing information in the FACTS database (Knight et al., 2022). However, the creation of the fuels management and forest disturbance dataset by Kramer et al. (2025) combined with bioregional-scale acoustic monitoring allowed us to conduct the first comprehensive assessment on the effects of different intensities of fuels management on spotted owls – or any mature-forest associated species.

We found diverging effects of fuels management based on fuels management intensity, where spotted owls were less likely to occur at sites with greater proportional area of heavier fuels management (>25 % canopy cover reduction) but insensitive to the proportional area of lighter fuels management at a survey site (<25 % canopy cover reduction). Moreover, when summed across the population, heavier fuels management led to an estimated loss of 65 occupied sites, while lighter management led to an estimated gain of 39 occupied sites, with a net estimated loss from fuels management of 26 occupied sites. Thus, our results were consistent with predictions that recent fuels management has negatively affected spotted owl occupancy, depending on intensity, but that the negative effect was small relative to severe fire. However, the maximum value of heavier fuels management reduced occupancy by a similar amount as the maximum value of severe fire, suggesting that implementation of heavier fuels management at the scale of recent severe fire may produce comparable declines in occupancy.

While heavier fuels management implemented at broader scales may cause similar near-immediate declines in spotted owl occupancy as severe fire, fire and forest modeling analyses suggest heavier fuels management may provide longer term benefits to spotted owls by curbing severe fire activity (Ager et al., 2007; Jones et al. 2024; Jones et al., 2021a; McGinn et al., 2025; Tempel et al., 2014). Importantly, McGinn et al. (2025) found that heavier fuels management provides net benefits to spotted owl occupancy within megafire footprints by reducing the adverse effects of severe fire compared to sites that were untreated. Further, fuels management activities in the Sierra Nevada are estimated to last around 20 years before fuel loads return to pre-management levels (Agee and Skinner, 2005; Stephens et al., 2012). In contrast, large, continuous patches of severe fire can prompt failed conifer regeneration, leading to type conversion, and effectively converting forested land to non-forested land (Collins et al., 2011; Dove et al., 2020). As such, negative effects of fuels management will likely be short term until vegetation regrows (Tempel et al., 2015), compared to potential long-term type conversion of essential spotted owl habitat attributed to uncharacteristic severe fire.

These diverging effects of management based on intensity suggest that managers can strategically combine management of heavier intensity and lighter intensity management to both balance negative occupancy influences while reducing risks to occupancy loss from severe fire (see *Management Implications* below). Given that spotted owls nest and roost in areas with large trees, high canopy cover, and understory density, management that significantly reduces canopy cover (i.e., "heavy management") will reduce occupancy, potentially by reducing nesting habitat quality, increasing predation risk, or producing unfavorable microclimates – as is potentially the case with drought/other. Conversely, management that creates greater structural heterogeneity may improve spotted owl habitat quality vis enhanced prey populations, as described above. Our categorization of management is delineated only on the degree of canopy cover reduction as quantified with MMI, leaving the effects of altering specific elements of forest structure, such as ladder fuels or canopy base height, less clear.

Further research could assess space usage, including foraging, nesting, and roosting, in response to fuels management activity leveraging the new fuels management dataset developed by Kramer et al. (2025) and assessing spotted owl responses to specific management activities. In addition, while spotted owls function as an effective indicator species for mature, closed forests, effects of fuels management on indicator species of other habitat preferences, such as the olive-sided flycatcher (*Contopus cooperi*) which are associated with mature, open forests, will be important to support broader avian communities (Brunk et al., 2025b). Nevertheless, our results demonstrate that the effects of fuels management vary by intensity, with lighter management having negligible effects on spotted owl occupancy compared to measurable negative effects of heavier management on spotted owl occupancy. However, the effects of fuels management were ultimately eclipsed by the negative effects of severe fire at both the site and population level.

5. Management implications

While reducing fuel loads and severe fire risk in the Sierra Nevada and conserving spotted owl habitat have long been perceived as conflicting objectives (Peery et al., 2017), our findings – in conjunction with previous work – suggests that resilience-oriented management could benefit spotted owl conservation. Specifically, fuels management activities that reduce canopy cover by < 25 % are unlikely to adversely impact spotted owl occupancy or populations, even when implemented broadly across home ranges and landscapes. Moreover, prior work indicates that forest structural components targeted in fuels management, such as increasing canopy base height, reducing ladder fuels, and reducing canopy bulk density can promote spotted owl foraging habitat (Wright et al., 2023). However, lighter intensity fuels management activities may not yield desired reductions in severe fire behavior if implemented exclusively (McGinn et al., 2025), whereas heavier intensity management that reduces canopy cover by > 25 % is more likely to curb severe fire (McGinn et al., 2025) but potentially reduce spotted owl occupancy. Nevertheless, our results, in conjunction with numerous previous studies, indicate that wildfire has had a greater impact on spotted owls than fuels management (Barry et al., 2025; Jones et al., 2021a; McGinn et al., 2025; Wright et al., 2023) and that fuels management, that reduces canopy cover by < 25 % are unlikely to negatively affect spotted owl populations (Ager et al., 2007; Jones et al., 2021a; McGinn et al., 2025; Tempel et al., 2015). Heavier fuels management activities, which can have negative effects on spotted owl populations, may need to be implemented judiciously to avoid detrimental effects, for example outside of high quality nesting habitat or within areas unsuitable for supporting denser forest conditions (ridgetops, south-facing slopes), in combination with lighter management activities, could promote spotted owl viability as the climate rapidly warms. Risks to spotted owls can be mitigated by targeting small- and medium-diameter trees while retaining large-diameters tress used for nesting (Jones et al., 2021a), roosting (McGinn et al., 2023), and foraging activities (Wright et al., 2023; Zulla et al., 2022, 2023).

While we have found evidence of synergies between fuels management and spotted owl conservation, the management of drought-prone and drought-affected forests and their impact on spotted owls are less certain and likely more complex. Managers often target drought-prone forests for reductions in tree densities to lower competition and water stress, and ultimately increase resistance to direct drought mortality and bark beetle-associated mortality (Bernal et al., 2023; Restaino et al., 2019; Vernon et al., 2018). While drought/other increased site occupancy for spotted owls, presumably by enhancing foraging conditions and/or as they may be the only remaining forested conditions in the vicinity of large-severe fires, further reductions in tree densities could negate these benefits in the future while reducing the secondary risk of loss of severe fire. Drought-related tree mortality likely reduces the quality and availability of nesting habitat, increases the likelihood and intensity of subsequent wildfires (Cansler et al., 2024; Stephens et al., 2018), and potentially exacerbates the adverse effects of severe fire on spotted owls. As such, we do not suggest a "hands-off" management approach that may promote drought-related tree mortality with the intention of promoting spotted owl habitat. Moreover, fuels management within areas already affected by extensive drought/other may be needed to reduce the risk of severe wildfires in the future, despite potential impacts to what may be high quality spotted owl foraging habitat. Clearly, more research is needed to understand the trade-offs associated with managing drought-prone and drought-affected forests in the context of changing fire regimes and mature-forest conservation.

6. Conclusions

Shifting disturbance regimes are altering mature forests and in turn, mature-forest associated species, prompting novel management dilemmas. Our work demonstrates that severe fire has led to greater declines in occupancy than lighter fuels management or heavier fuels management. Additionally, our work, in conjunction with other recent studies, suggests strategic implementation of management at varying intensities may benefit spotted owl populations. There appears to be synergy in the conservation of mature-forest species and forest restoration, and intentional fuel management can promote success for both objectives. Further research could evaluate direct effects of distinct management activities, explore the nuanced effects of drought and other canopy reducing disturbance, and expand management and disturbance analyses to avian communities within the Sierra Nevada.

CRediT authorship contribution statement

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Funding

This work was funded by the USDA Forest Service Region 5 and the National Fish and Wildlife Foundation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Michèle Slaton, Alexander Koltunov, and Josh Barry for their helpful comments on the disturbance dataset creation and design. In addition, we thank the many field technicians who helped deploy acoustic recorders in 2021 and 2022 and made this analysis possible.

Data availability

The data that has been used is confidential.

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